

Host Habitat Preference of *Fopius arisanus* (Hymenoptera: Braconidae), a Parasitoid of Tephritid Fruit Flies

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ABSTRACT The braconid parasitoid *Fopius arisanus* (Sonan) (Hymenoptera: Braconidae) is a candidate for augmentative biological control of tephritid fruit flies. In the Puna district of Hawaii Island, *F. arisanus* parasitized 41–72% of oriental fruit flies, *Bactrocera dorsalis* (Hendel), in wild common guava, *Psidium guajava* L.; strawberry guava, *Psidium cattleianum* Sabine; and tropical almond, *Terminalia catappa* L. In commercial papaya, *Carica papaya* L., in the same region, parasitism was only 22% in tree-collected fruit and 3% in ground-collected fruit. The low level of parasitism in papaya suggests that wild parasitoids may not track the host flies well in commercial fruit and that augmentative parasitoid releases could potentially increase parasitism and thus suppress host fly populations in this habitat. The very low parasitism in ground-collected papaya suggests that *F. arisanus* may avoid foraging on ground fruit. Field cage experiments support this hypothesis. Numbers of females observed on tree fruit were two-fold higher than on ground fruit in small cages and 4–6-fold higher in large cages. In an experiment conducted in a papaya orchard, sentinel fruit was placed within the canopy, on the trunk, or on the ground. Parasitism was significantly higher in the canopy-placed fruit in only one of three trials. This variable response to ground fruit in the field suggests that augmentative parasitoid releases may have a significant, albeit reduced, effect on host populations under conditions of poor sanitation.

KEY WORDS biocontrol, egg–pupal parasitoid, host location, Tephritidae

Several studies have demonstrated that augmentative release of opiine braconid parasitoids can suppress tephritid fruit fly populations. In the field, Mediterranean fruit fly, *Ceratitidis capitata* (Wiedemann), was suppressed by *Diachasmimorpha tryoni* (Cameron) in Maui, HI (Wong et al. 1991, 1992), and *Anastrepha* spp. were suppressed by *Diachasmimorpha longicaudata* (Ashmead) in Florida and Mexico (Sivinski et al. 1996, Montoya et al. 2000). Additionally, field cage studies have demonstrated suppression of melon fly, *Bactrocera curcurbitae* (Coquillett), by *Psytalia fletcheri* (Silvestri) (Vargas et al. 2004) and of *C. capitata* by *Fopius arisanus* (Sonan) and *D. krausii* (Fullaway) (Rendon et al. 2006). All of these are larval–pupal parasitoids, except for *F. arisanus*, which is an egg–pupal parasitoid. Other augmentative releases have failed to reduce host populations (Purcell 1998), but the reasons for this are not always clear. One reason for failure could be that a substantial proportion of the host population is not susceptible to parasitism.

Fopius arisanus is a very efficient parasitoid of tephritid fruit flies (Clausen et al. 1965, Rousse et al. 2005), with parasitism levels sometimes averaging >50% in the field (Vargas et al. 1993, Purcell et al. 1994, Vargas et al. 2007). In Hawaii, its primary host is the oriental fruit fly, *Bactrocera dorsalis* (Hendel) (e.g.,

Vargas et al. 1993), but it also parasitizes *C. capitata* (Haramoto and Bess 1970), the solanaceous fruit fly *Bactrocera latifrons* (Hendel) (McQuate et al. 2007), and *B. curcurbitae* (Bautista et al. 2004).

Purcell et al. (1994) observed a decrease in the number of *F. arisanus* emerging from guava fruit as they remained on the ground. If this is due to avoidance of searching on ground fruit, the effect of parasitoids on host populations may be diminished when poor sanitation is practiced (Liquido 1993).

In this study, we evaluated the impact of *F. arisanus* on *B. dorsalis* in papaya orchards and wild hosts, as part of the Hawaii Fruit Fly Areawide Pest Management program (Vargas et al. 2003). Specifically, we determined parasitism levels in various fruit in the Puna district, Hawaii Island, and tested the preference of mass-reared *F. arisanus* for tree and ground fruit in field cage and field experiments. We discuss the relevance of our results to the integration of biological control with cultural practices and the potential for fruit fly suppression through augmentative releases of parasitoids.

Materials and Methods

Field Survey. We collected samples of fruit at 3-wk intervals from October 2005 through March 2006 at 41 sites in the Puna district, Hawaii Island (Fig. 1). Fruit

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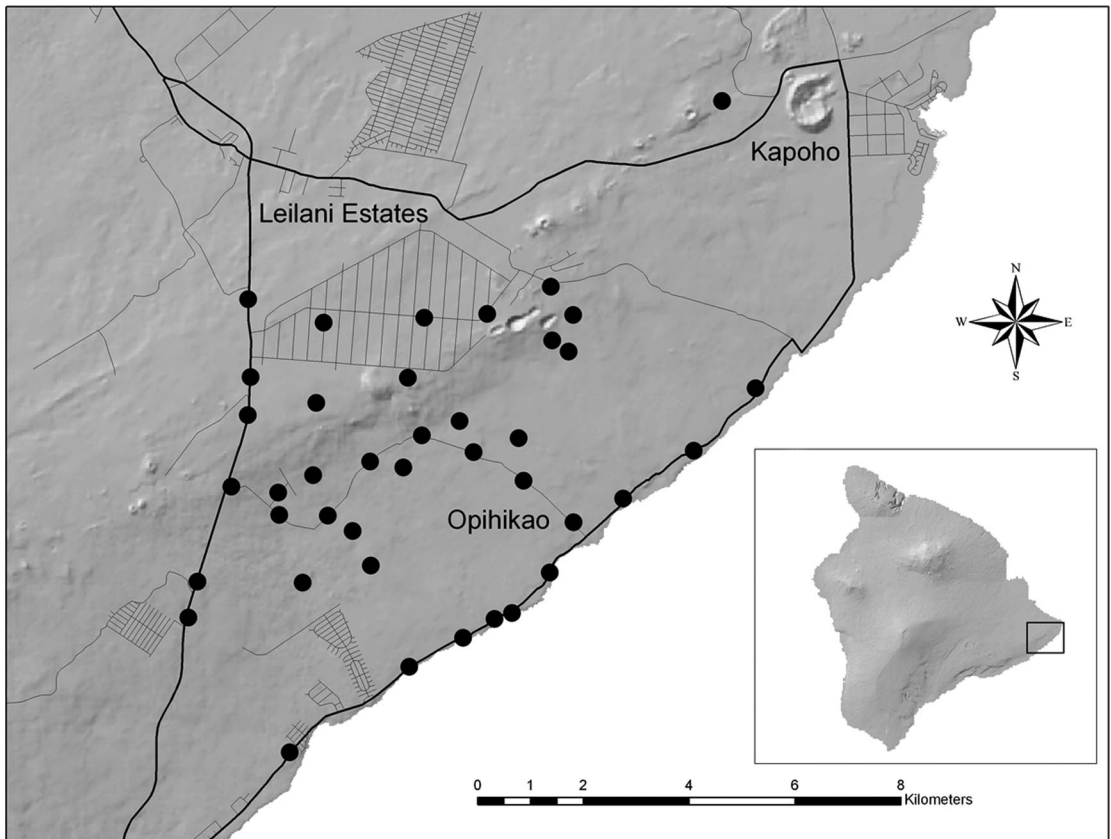


Fig. 1. Fruit collection sites in the Puna district, Hawaii Island.

sampled included common guava, *Psidium guajava* L.; red and yellow strawberry guava, *Psidium cattleianum* Sabine; tropical almond, *Terminalia catappa* L.; and papaya, *Carica papaya* L. Guavas and tropical almond are the most common wild hosts of *B. dorsalis*, and papaya is the primary agricultural commodity in Puna. At each site, we took separate samples of intact ripe fruit from the tree and from the ground, depending on fruit availability. For tropical almond, only ground fruit were collected, because canopies were too high to reach tree fruit. Numbers of fruit per sample were 1–11 for common guava, 3–50 for red strawberry guava, 4–29 for yellow strawberry guava, 6–17 for tropical almond, and 1–3 for papaya.

Fruit samples were placed on 0.7 liter of sand within two stacked 5-liter buckets (hi-plas, Pasadena, CA) (the inner bucket with screened holes to allow drainage of fruit juices) covered with a fine-mesh screened lid, and they were maintained at ambient temperatures. Sand was sieved weekly for 4 wk, and tephritid larvae and puparia were held in fine-mesh screened, 1-liter containers (hi-plas) with moist sand (60 ml of water/liter sand) until eclosion. For papaya samples, puparia of *B. dorsalis* and *B. cucurbitae* were held in separate containers (*B. cucurbitae* does not infest the other host fruit collected). No parasitoids were recovered from *B. cucurbitae*, and it is not considered

further in this article. Emergence containers were maintained at $27 \pm 1^\circ\text{C}$ and 60–85% RH.

For estimation of parasitism levels, we considered only samples from which 10 or more insects emerged (167 of the 395 samples collected). For each sample, we estimated parasitism of *B. dorsalis* as (no. of parasitoids emerging)/(no. of *B. dorsalis* + parasitoids emerging). This proportion was arcsine square-root transformed before analysis. Levels of parasitism by *F. arisanus* were compared among fruit types and between fruit positions (tree versus ground) by one-way analyses of variance (ANOVAs). When the ANOVA was significant ($P < 0.05$), means were compared by the Tukey–Kramer honestly significant difference (HSD) test. Analyses were performed with JMP software (SAS Institute 2005).

Field Cage Experiments. *Fopius arisanus* were obtained as pupae from a colony maintained for ≈ 90 generations at the rearing facility of the U.S. Pacific Basin Agricultural Research Center (PBARC) in Honolulu, HI. They were reared in 26-cm³ wooden-framed fine-mesh screened cages at $25 \pm 1^\circ\text{C}$, 55–75% RH, and constant light, and they were provided with a constant supply of honey-agar and water. *B. dorsalis* were obtained from a colony maintained for ≈ 240 generations at the PBARC rearing facility.

We tested the response of *F. arisanus* to "sentinel" fruit containing *B. dorsalis* eggs. We chose to use papayas for this purpose because they are available commercially year-round. Single papayas were placed in 20-cm³ screened cages, each with 20 \approx 17-d-old *B. dorsalis* females, for 24 h. Flies were provided with water, sugar as a carbohydrate source, and yeast hydrolysate (USB Corporation, Cleveland, OH) as a protein source. In a preliminary experiment, fruit presented to *B. dorsalis* in this manner yielded a mean of 159 puparia, confirming that they were infested.

Small Cage Test. Fifty 10-d-old *F. arisanus* females were released into a 2-m³ fine-mesh cage (BioQuip Products, Inc., Rancho Dominguez, CA) containing a potted common guava tree and two sentinel fruit enclosed in BirdBlock netting (Easy Gardener, Inc., Waco, TX). One fruit was hung within the foliage ("tree fruit") and a second fruit was placed on the ground ("ground fruit") adjacent to the pot. Parasitoids were released into the cage at 1000 hours by gently opening a 20-cm³ screened cage on the ground and allowing them to alight. We recorded the number of females on each fruit every h from 1100 through 1600 hours. This experiment was replicated five times.

Large Cage Test. Given the high probability of random landing on less preferred fruit in small field cages, any preference between tree and ground fruit should be more pronounced in a larger arena. Therefore, we conducted a second experiment in a large field cage measuring 15 by 6 by 2.5 m. Sentinel fruit were placed in four rows containing two trees each. One fruit was hung with the foliage of one tree, and another fruit was placed on the ground at the base of the second tree within each row, for a total of four tree fruits and four ground fruits. Position of the fruit (tree or ground) was alternated among rows. All fruit were placed at the side of the tree facing the center of the cage. Two hundred 10-d-old *F. arisanus* females were released at the center of the cage at 1000 hours as described for the first experiment. Mean numbers of parasitoids on tree and ground fruit were calculated for each h from 1100 through 1600 hours. This experiment was replicated four times.

Both experiments were analyzed by repeated measures ANOVA, following square-root transformation, with JMP software (SAS Institute 2005).

Field Experiment. Sentinel fruit were prepared as in field cage experiments. *F. arisanus* were obtained as pupae from the PBARC rearing facility, and they were reared in 60-cm-diameter by 64-cm-hgh cylindrical cages with fine-mesh sides and plastic tops and bottoms at 24 \pm 2°C, 60–80% RH, and a photoperiod of 12:12 (L:D) h. Spun premium honey (Bradshaws, Sioux Falls, IA) was applied to the outside of the cage two to three times a week, and water was provided constantly in 450-ml plastic cups with cotton wicks.

In a commercial papaya orchard in Kapoho, Hawaii Island, we placed sentinel fruit at three heights: on the ground, on the trunk at \approx 2 m, and within the canopy at \approx 4 m. Fruit were placed within 15- by 13- by 13-cm metal-screen (2.5-cm mesh) cages to prevent vertebrate damage. Ground and trunk samples were at-

tached to the tree trunk with zip-ties, and canopy samples were hung on the tree by using an extendable pole. One fruit of each height treatment was placed in each of four rows, spaced 9 m apart, in a randomized block design. Treatments within rows were placed \approx 5 m apart.

After placement of the experimental fruit, we released 10-d-old *F. arisanus* 30 m upwind of the first sentinel fruit in each row. For each row, a single cylindrical cage was opened, and its components were laid on the ground. Parasitoids were allowed to disperse for 20 min, after which we gently shook off any remaining parasitoids. Fruit were collected from the field after 24 h and handled as described above for the parasitoid survey.

We repeated this experiment three times, on 11, 18, and 25 October 2006. Based upon the estimated number of pupae, the eclosion rate and sex ratio in quality control samples, and the number of dead parasitoids in the cages, we estimated that the number of females released for each trial was 11,050, 10,980 and 10,280, respectively.

For each fruit, we estimated the parasitism level as (*F. arisanus* eclosing) (*B. dorsalis* eclosing + *F. arisanus* eclosing). This proportion was arcsine square-root transformed, and each replicate was analyzed by one-way ANOVA. When the ANOVA was significant ($P < 0.05$), means were compared by the Tukey-Kramer HSD test. Analyses were performed with JMP software (SAS Institute 2005).

Results and Discussion

Parasitoid Abundance in Various Host Fruit. In total, 2,804 opiine braconid parasitoids were recovered in the survey. Of these, 2,751 (98.1%) were *F. arisanus*, 34 (1.2%) *D. longicaudata*, and 19 (0.7%) *Psytalia incisi* (Silvestri). Mean parasitism of oriental fruit fly by *F. arisanus* ranged between 41 and 72% in tree and ground samples of all wild fruit, including common guava, strawberry guava, and tropical almond (Table 1). This is similar to the 38–62% parasitism reported for this species from common and strawberry guava on Kauai Island (Vargas et al. 1993) and 43–51% from common guava on Hawaii Island (Purcell et al. 1994).

F. arisanus parasitism levels were significantly different among fruit types for both tree fruit ($F = 4.54$; $df = 3, 96$; $P = 0.005$) and ground fruit ($F = 31.07$; $df = 4, 60$; $P < 0.0001$). For tree-collected samples, parasitism in commercial papaya, averaging 22%, was significantly lower than in common guava. For ground-collected samples, parasitism in papaya, averaging only 3%, was significantly lower than in all other fruit. This low parasitism suggests that *F. arisanus* may not track the host populations well in commercial fruit, which is consistent with the observation of Vargas et al. (1993) that parasitism levels are lower in commercial common guavas than in wild fruit.

When parasitism levels are naturally low, augmentative parasitoid releases could cause an increase in parasitism, and thus potentially significantly affect

Table 1. Parasitism of *B. dorsalis* by *F. arisanus* in fruits sampled in Puna, Hawaii Island (2005–2006)

Fruit	Location	Samples	Fruit/ sample	Eclosion/ kg fruit ^a	% Parasitism (mean \pm SEM)	F	P
Common guava	Tree	52	7.6	67.8	54.7 \pm 4.61	5.64	0.020
	Ground	29	8.2	32.8	71.8 \pm 4.88		
Yellow strawberry guava	Tree	10	16.5	72.4	40.8 \pm 9.26	0.02	0.88
	Ground	3	18.0	110.4	43.6 \pm 18.84		
Red strawberry guava	Tree	25	29.0	98.5	47.5 \pm 6.07	0.11	0.74
	Ground	7	27.1	73.0	43.8 \pm 13.82		
Papaya	Tree	14	2.4	70.4	22.4 \pm 7.80	7.52	0.010
	Ground	20	2.7	108.6	3.3 \pm 2.00		
Tropical almond	Ground	7	13.1	135.9	61.6 \pm 6.36		

Statistics are for one-way ANOVA comparing parasitism in tree and ground fruit for each fruit type.

^a Total *B. dorsalis* and parasitoids eclosing, excluding *B. cucurbitae*.

host fly populations. In Waimea, Hawaii Island, augmentative releases of *F. arisanus* during 2003–2004 increased parasitism levels in common and strawberry guava from 7 to 13% in the prerelease period to 48–56% during the release period (R.I.V., unpublished data). Assuming similar levels of parasitism could be reached, augmentative releases could potentially more than double the level of parasitism in commercial papaya.

Preference for Tree versus Ground Fruit. The extremely low parasitism in ground-collected papaya, significantly lower than in tree-collected fruit (Table 1), suggests that *F. arisanus* may avoid foraging on ground fruit. Evidence for such a preference was presented by Purcell et al. (1994), who found decreased parasitism by *F. arisanus* the longer common guava fruit remained on the ground. Although the high levels of parasitism in ground-collected guava and tropical almond in the current study seem to contradict this hypothesis, these wild fruit ripen on the tree, and most of the fly infestation probably occurs before the fruit falls to the ground. Thus, the majority of parasitism observed in ground-collected fruit likely occurred while these fruit were still on the tree. In contrast, commercial papaya fruit are regularly felled from the trees when they are still unripe, either because they are deformed or to leave space for other fruit to grow (A.E., unpublished data). Fruit felled when they are green are initially infested at a very low level (Liquido et al. 1989), but they may subsequently ripen and become infested on the ground. Parasitism in these fruit would necessarily have to occur on the ground.

In small field cages, the number of females observed on tree fruit was approximately double that on ground fruit (Fig. 2A; $F = 10.86$; $df = 1, 8$; $P = 0.011$). In large field cages, the preference for tree fruit was even stronger, with 4–6 times more females on tree versus ground fruit at the various times (Fig. 2B; $F = 14.43$; $df = 1, 6$; $P = 0.009$).

These experiments confirm that *F. arisanus* females prefer to forage on tree fruit. We consider it remarkable to be able to observe such a preference in a small arena, where the probability of landing by chance on a particular fruit is high. Furthermore, these parasitoids have been reared for many generations in the laboratory, where they parasitize eggs placed at the floor of the cage (Bautista et al. 1999). Thus, laboratory

rearing may have selected for parasitoids that move down in their search for oviposition sites. Despite this possible selection, the preference for searching for hosts within the canopy has been maintained.

In the field experiment, parasitism was relatively low, averaging 0.2–16.0% in the various treatments (Fig. 3). This experiment was not designed to evaluate the efficiency of augmentative releases. Rather, it gives an estimate of the relative response to fruit at different heights. The number of insects (*B. dorsalis* plus *F. arisanus*) emerging from fruit ranged from 55 to 509, and it was not significantly different among treatments in any trial (one-way ANOVA following

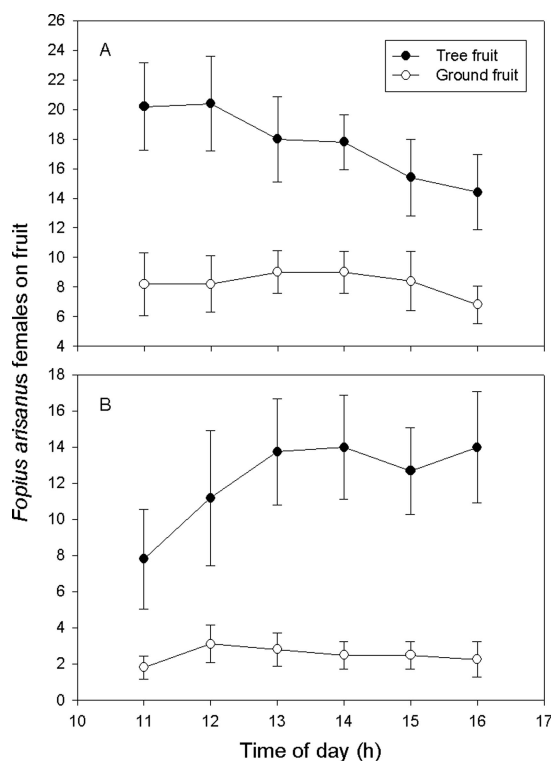


Fig. 2. Mean number of *F. arisanus* females observed on tree- and ground-placed sentinel fruit in (A) small (2-m²) and (B) large (15- by 6- by 2.5-m) field cages. Error bars represent ± 1 SEM.

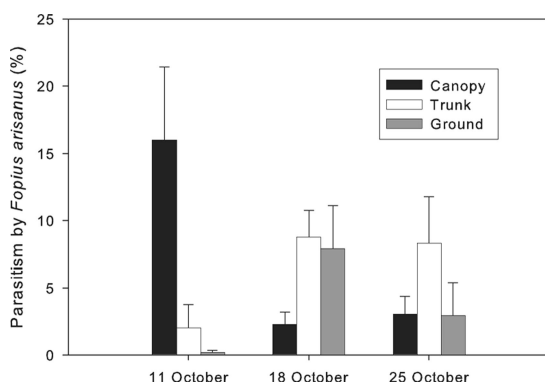


Fig. 3. Mean percentage of parasitism of *B. dorsalis* by *F. arisanus* in sentinel fruit placed in a papaya orchard within the canopy, on the trunk and on the ground. Error bars represent 1 SEM.

square-root transformation). In the first trial, parasitism levels were significantly different among treatments ($F = 10.41$; $df = 2, 9$; $P = 0.0046$), with higher parasitism in fruit placed in the canopy versus fruit on the trunk or on the ground (Fig. 3). However, there were no significant differences in parasitism among treatments in the second ($F = 2.71$; $df = 2, 9$; $P = 0.12$) or third ($F = 1.62$; $df = 2, 9$; $P = 0.25$) trials (Fig. 3). Thus, the preference for tree fruit observed in the field cage experiments is occasionally, but not always, manifested in the field.

***F. arisanus* and Integrated Pest Management (IPM) in Papaya.** *B. dorsalis* is a serious pest of ripe papaya in Hawaii, prompting farmers to pick fruit when it is unripe to avoid infestation (Liquido et al. 1989), thereby reducing the value of their crop. The Hawaii Fruit Fly Area-wide Pest Management program is designed to suppress fruit flies below economic thresholds while reducing the use of organophosphate insecticides (Vargas et al. 2003). An important component of this program is the maintenance of significant populations of biological control agents. The avoidance of ground fruit by *F. arisanus* suggests that the impact of wild parasitoids on *B. dorsalis* populations is significantly reduced when there is poor sanitation in the papaya orchards, i.e., when fruit is left on the ground (Liquido 1993), because a large proportion of the hosts would not be susceptible to parasitism. Thus, good sanitation is essential to reap benefits from natural biological control in an integrated pest management (IPM) program (Klungness et al. 2005).

Similarly, if released parasitoids do not forage on ground fruit, augmentative releases of *F. arisanus* may not be efficient when poor sanitation is practiced. The field experiment demonstrates that the efficiency of foraging on ground fruit is variable and that it may depend on factors such as environmental conditions or parasitoid quality. Identification of these factors warrants further investigation. This variable response to ground fruit in the field suggests that augmentative parasitoid releases may have a significant, albeit reduced, effect on host populations in conditions of poor sanitation.

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